

ON THE CONNEXION BETWEEN STYLE-SAC AND INTESTINE
IN GASTROPODA AND LAMELLIBRANCHIA.

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So much has been written in the past upon the crystalline style in the Mollusca that some excuse is necessary for a further excursion into this subject. Some observations which I have recently published seem, however, to be of sufficient interest to warrant fresh morphological discussion on this structure.

The problem for discussion is the significance of a narrow, longitudinal slit placing the sac of the crystalline style in communication with the pyloric part of the intestine. This communication between the sac and the intestine has been described previously in the Lamellibranchia, and I have been able recently to demonstrate its occurrence in the "Hydrobiid" genera of Gastropoda, *Paludestrina* and *Hypsobia* (Robson, 1920-21-22).

The relation between style sac and intestine in the Lamellibranchia has been very fully discussed by Matthias,¹² who distinguishes three groups within that class. In these we find a progressive separation of the pyloric and cœcal (style sac) elements of the stomach. In forms like *Leda* and *Yoldia Arca*, *Ostrea*, and the *Septibranchia* the pylorus and style sac are in wide and open communication with each other. In *Modiolaria* and *Jouannetia* this communication is very much restricted, only a narrow cleft remaining. Finally, in *Teredo*, *Pholas*, *Dreissensia*, and others, the sac and the pylorus are completely separated. E. Ghosh⁶ has described several apparent instances of the second condition in the Solenidæ, and has discussed them with regard to the Lamellibranchia as a whole. His account is a little puzzling in several cases. Under *Solen* (e.g. p. 52) he says: "Cœcum arising from the ventral aspect of the pylorus," and does not specify whether there is an open communication, though one might suppose from his introduction (p. 50) that there is not. The same lack of precision is to be noted under *Subcutellus* (p. 61).

Burne³ has described a condition representing the first of Matthias' stages in *Anatina elliptica*.

The occurrence of a style and style-sac in Gastropoda has been discussed by several authors, notably by Moore¹³ (1898) and M. F. Woodward²¹ (1893). A summary of the known distribution and modifications of these structures has not been given, so that I take this opportunity of drawing together all the records that have been accessible to me. The following list is probably not exhaustive, though it covers a wide enough field to give an idea of the distribution.

Docoglossa.

i. Style present in various forms; Pelseneer.¹⁶ The only case I am acquainted with is that of *Patella* (Gibson, Trans. Roy. Soc. Edinburgh, xxxii, 1885), to which Professor Pelseneer has kindly drawn my attention. I have been unable to discover other cases in the fairly copious literature of this group.

Rhipidoglossa.

ii. Style present in *Fissurella*; Haller⁹ (1888). There is apparently no special sac in this form, the style being pyloric in origin and position.

iii. (?) Style present in *Trochus turritus* (probably = *T. matoni*, Peyr.); Collier (1829). There is neither style nor sac recorded by Haller⁹ (1894) and Randles (1905) in their more exhaustive examination based upon several species, and though this case has figured in several textbooks, I am inclined to think some other form is indicated, as may well be the case in such an early writer as Collier.

Tenioglossa.

iv. A cœcum more or less pyloric in position present in *Ampullaria*; Bouvier.¹ No style is recorded, and Bouvier does not discuss the possibility of this cœcum being a style-sac. But from its position it would seem likely to have this function.

v. A style present in the "conoid" part of the intestine (i.e. pylorus) in *Cyclostoma*; Garnault.⁷

vi. A style present in *Lithoglyphas*; Von Ihering.¹⁷ It is found "im magen"; but no further details are given.

vii. A style present in *Bithynia*; Moquin Tandon.¹⁴ It is found "dans l'estomac", and no further details are given. But the figure of *B. tentaculata* given by Simroth seems to show a definite sac.

viii. A sac present in *Rissoa*; Simroth.¹⁹ No style has been recorded as far as I can find, but the figure given by Simroth seems to show a definite sac.

ix. A style and sac present in *Paludestrina*, Robson¹⁸ (1920-22).

x. A style and sac present in *Hypsobia*, Robson¹⁸ (1921). The sac is in communication with the pylorus by means of a narrow slit in ix and x. It is impossible to say whether such a connexion occurs in vii and viii, as only the surface anatomy is figured.

xi. A style and sac completely (?) separated from the pylorus in *Bythinella dunkeri*; Bregenzer.²

xii. A style and sac found completely separated from pylorus in *Adeorbis*; Woodward²¹ (1899), *Turritella*; Randles¹⁷ (1902), *Typhobia*, *Spekia*, *Tanganyicia*, *Nassopsis*, *Paramelania*, *Chytra*, *Limnotrochus*, *Bythoceras*; (Moore,¹³ 1898-9, Digby⁸), *Pterocera* (Huxley,¹⁰ Woodward,²¹ 1893).

I have been unable to find any satisfactory references to the

presence of a style or sac in the Rhachiglossa or Toxoglossa. From the figures of *Nassa*, *Buccinum*, and *Murex*, given by Simroth,¹⁹ there would appear to be no sac large enough to lodge a style, though the slight hollowing out between cardiac and pyloric orifices in *Murex* is referred to by him as a cœcum. Collier's statement that a style occurs in *Murex vertagus* may be regarded in the same light as his statement regarding *Trochus turritus*, though we have more positive evidence in this case, as *vertagus* is a well-known specific name of the *Vertagus* subgenus of *Cerithium* and at least one early author (cf. Tryon²⁰) has referred a *Cerithium* to *Murex*! We have seen above that a style is very largely restricted to the Tænioglossa, to which group *Cerithium* is referred.

We have now to discuss shortly a few ambiguous cases before proceeding to our general considerations. As a preliminary to this a certain amount of definition is necessary. We have considered so far cases where we find either a definite style or a sac lying alongside the pylorus, and sometimes communicating with the latter, which, for various obvious reasons, may be considered as the sac in which the style is formed. This definition is necessary because the style is a transitory structure, disappears under certain physiological conditions, and is rapidly dissolved by fixation reagents. In its absence we may argue from the presence of the characteristic sac. But on this point due discrimination should be exercised before all pyloric cœca are accepted as style sacs. For that reason I have qualified the case of *Ampullaria*. A similar caution has to be exercised with regard to the so-called *flèche tricuspidè*. Moore¹⁴ (1898) pointed out the error of identifying this structure with the crystalline style, though he fell into the error of assuming that the *flèche* of older authors really meant the whole cuticular lining of the stomach, which had become detached from the stomach wall. It would seem, however, that the *flèche* is the strongly marked cuticular ridge often found in the wall of the stomach of many Prosobranchs.

We have described several obviously doubtful cases above, such as *Lithoglyphus*, in which, although we know a style occurs, the precise position of the latter is doubtful. There are, in addition, certain cases in which we should suspend judgment as to whether a style occurs at all. In *Concholepas* Haller⁹ (1888, pp. 110, 111), apparently considers there is a style owing to the similarity between the area assumed to secrete the style in that genus and in *Fissurella*. He found no style, however, and there is apparently no cœcum.

There is, finally, a third category of doubtful cases. Collier states that there is a style in *Strombus*, and Haller⁹ (1893) refers to a cœcal outgrowth in that genus and in *Rostellaria*; though he does not refer to any style. Woodward (1893, p. 147) says that this cœcum is obviously the homologue of the crystalline style-sac of *Pterocera*. I do not consider that this is so obvious as Woodward thought.

If Haller's figures are studied the œsophagus will be seen to intervene between the cœcum and intestine and the former does not occupy the same position as it does in *Pterocera*.

With these reservations we may now consider these structures from a wider standpoint. We first of all see that the style, either enclosed in a sac or free, is a fairly widely distributed feature in Prosobranchs, though it is probably limited to the Docoglossa, Rhipidoglossa, and Tænioglossa. We next see that there is an extraordinary parallelism between the Gastropoda and Lamellibranchia in the ultimate separation of the style-sac from the pylorus and the occurrence of intermediate types in which the separation is incomplete. Thus *Yoldia*, *Arca*, and *Mytilus* on the one hand, and *Fissurella* and *Cyclostoma* on the other, represent the stage when the style is either free in the pylorus, or a specialized part of the latter is still in wide communication with the intestinal part. Next, we have *Modiolaria* among Lamellibranchia and *Paludestrina* and *Hypsobia* among Gastropoda in which the communication is very much restricted. Finally, we have *Pholas* and *Donax* on the one hand, *Adeorbis*, *Typhobia*, and *Pterocera* on the other, in which the style-sac is fully differentiated and completely separated from the intestine.

We have hitherto spoken as though the style-sac was differentiated off the pyloric part of the intestine. The reverse possibility is suggested by Ghosh.⁸ According to his view it is just as likely that the style-sac evolved as an outgrowth from the stomach independently of the pylorus, such a separate style-sac being "present in the ancestral forms before the evolution of the present class" (l.c. p. 73). Such a suggestion deserves serious consideration, though I do not consider it indicates the more likely course of events. In the Gastropoda the evidence seems to favour the view that the course of development was from original unity with the pylorus to subsequent separation. Thus we have a style only in *Fissurella* and *Cyclostoma*, while among the rest of the Tænioglossa we have the less specialized Paludestrinidæ showing a partly differentiated sac and the more specialized *Pterocera* and *Turritella* with the sac separated. This part of the argument conceivably might be met by pointing out that *Adeorbis*, which has a separate style-sac, is considered to have affinities with the Rissoidæ, which are again fairly akin to the Paludestrinidæ.

In the Gastropoda the morphological status of the various suborders and families is fairly clear, and one may be tolerably certain as to the position of a form used in such an argument as the above. With the Lamellibranchia, however, the matter is otherwise. We know that some of the Protobranchia are certainly primitive, but beyond that it is very difficult to be absolutely sure that the taxonomic position assigned to an animal is any index of its real morphological status. As a consequence, generalizations about forms exhibiting modifications of a certain character are apt to be very

misleading. Thus, from Matthias' account¹² we find that certain Eulamellibranchs agree with the Protobranchia in having the style-sac in open communication with the intestine, while a Filibranch like *Phaseolicama* has a separate sac; and the Septibranchia apparently are in the same condition with regard to this character as the Protobranchia. This, of course, leaves us with two alternative conclusions, either that the taxonomy of the Lamellibranchia is as far off as ever from a rational order, or that, as several authors have suspected, there has been independent evolution within the various groups. I hope to discuss these alternatives in another place; but in the meantime, while we are confronted with such a dilemma, we can only content ourselves by pointing out that the Protobranchia which are clearly the most primitive do not have a differentiated style-sac, and that they agree therein with the more primitive Gastropoda. That a good deal of independent evolution takes place in the smaller groups is evident from a comparison of *Paludestrina* and *Bythinella* among the Prosobranchs. But, having regard to the issue raised by Ghosh's suggestion, the most important point in the morphological series is the one in the Lamellibranchia and Prosobranchs, where we find the style-sac undifferentiated. Whichever course was followed by this structure in its evolution, we may safely assert in conclusion that there has been a remarkable and close parallelism between the Gastropoda and Lamellibranchia. We may, at this point, recall that a pyloric cœcum is present in the Scaphopoda, though whether a style is secreted in it is very doubtful. Even if we may not bring the Scaphopoda into the argument, the remarkable similarity between Gastropoda and Lamellibranchia with regard to the evolution of the style-sac (a similarity called *homoplasy* by Lankester) is another instance of the fundamental unity that characterizes the Mollusca.

Many authors have constructed genealogical trees illustrating the relationships of the classes of Mollusca. I do not wish to add yet another sapling to that adventurous plantation. But I think we may allow ourselves the following conclusions from these observations:—

(1) The Gastropoda and Lamellibranchia which otherwise suggest by their structure a very remote ancestral point of separation have in respect of their digestive system retained in common (a) a singularly characteristic structure and (b) equal developmental potentiality with regard to it; and

(2) That with regard to the Lamellibranchia the general morphological importance of the style-sac as set forth above renders that structure an important factor in the classification of that group as Matthias has suggested. It has yet to be seen whether our taxonomy is wrong and the class requires regrouping, or whether there has been independent evolution on a large scale leading

to remarkable instances of convergence. Any future attempts to investigate the taxonomy of this group as a whole must deal with a large number of correlated characters, one of which should be the structure discussed above.

A fact of considerable interest for consideration under the first part of this conclusion is the very remarkable similarity between the longitudinal grooves found in the wall of the style-sac of *Bythinella* and *Paludestrina*, and in certain Lamellibranch genera (Nelson,¹⁵ Edmondson⁶). But the subject requires more investigation before it can be properly utilized in this context.

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¹⁹ Simroth, H., 1901, Bronn's Thierreich (2nd ed.), Bd. 3.

²⁰ Tryon, W., 1887, Man. Conch., ix (under *Cerithium aluco*).

²¹ Woodward, M. F., 1893, Proc. Mal. Soc., i; 1899, ib. iii.